THE SYSTEMATIC POSITION OF THE GENUS *AGABETES* CROTCH WITHIN DYTISCIDAE (COLEOPTERA, ADEPHAGA)

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Quaestiones Entomologicae
26: 221–238 1990

ABSTRACT

Structural features of the ovipositor, its musculature and associated structures are described and used to assess the phylogenetic position of Agabetes *Crotch. Assignment to the subfamily Colymbetinae is not tenable because it is based on plesiomorphic character states. Rather it should be assigned to the subfamily Agabetinae which is the sister group to Laccophilinae based on six synapomorphies: (1), ventral teeth on genital appendages VIII; (2), genital appendages divided proximally into three separate arms; and (3), with the ventromedial arm articulated with gonocoxosterna; (4), presence of muscle 26, and unique origins; (5), of muscle 28 which is the retractor muscle of genital appendages VIII; and (6), of muscle 37 on lateral arms of genital appendages VIII.*

ZUSAMMENFASSUNG

Die Anatomie des Ovipositors mit seiner Muskulatur und Anhangsorganen von Agabetes acuductus *Harris wird beschrieben. Die Merkmale werden zur Klärung des systematischen Stellung der Gattung* Agabetes *Crotch innerhalb der Dytiscidae heranzgezogen. Die bisherige Zuordnung zur Unterfamilie Columbetinae beruht auf plesiomorphen Merkmalen. Auf Grund folgender sechs Synapomorphien ist die Unterfamilie Agabetinae als Schwestergruppe der Laccophilinae aufzufassen: (1) Genitalanhänge VIII mit ventralen Zahnreihen; (2) Genitalanhänge VIII cranial in drei Teile aufgespalten, der (3) ventromediane unpaare Fortsatz besitzt jederseits ein Gelenk mit den lateralen Gonocoxosterna; (4) Vorhandensein des Depressors der Genitalanhänge VIII (M 26) und der Ursprung (5) des Retractors (M 28) zusammen mit der Protractor der Genitalanhänge (M 37) an den Lateralfortsatzen (6). Die Bedeutung anderer Merkmale für die Phylogenie dieser Unterfamilien der Dytiscidae wird diskutiert.*

INTRODUCTION

Crotch (1873) proposed the genus *Agabetes* to receive the single Nearctic species, *Colymbetes acuductus* Harris. Zimmermann (1920) assigned *A. acuductus* to the tribe Copelatini of the subfamily Colymbetinae. However, at an earlier date, Van den Branden (1885) had provided the family-group name Agabetini for this genus. Presumably, Van den Branden did this because Sharp (1882) had noted that *Agabetes* did not show much affinity to other groups of colymbetines. Many North American authors (*e.g.*, Arnett 1968, Dillon and Dillon 1972) have used the tribal rank of Agabetini and placed it within the subfamily Colymbetinae. Thus for many years, *Agabetes* was assigned to various groups of Colymbetinae.

Burmeister (1976) first demonstrated a relationship among *Agabetes* and *Laccophilus* Leach (Laccophilinae), based on apomorphic structural features of female genitalia. Subsequently, Nilsson (1989) described a second species of *Agabetes*, *A. svetlanae*, from Iran. He discussed certain features of adults and larvae of *Agabetes* and placed it within the tribe Agabetini Van den Branden as the sister group to Laccophilini Bedel, both within the subfamily Laccophilinae Bedel. Nilsson (1989) noted that I had studied members of only one genus (*Laccophilus*) of 11 genera presently assigned to Laccophilinae (Brancucci 1983).

I did not examine any specimens of *A. svetlanae* which, according to Nilsson (1989), is very similar to *A. acuductus*. Therefore, structural features of adults of *A. acuductus* are very likely generic features.

The purposes of this paper are: (1), to present a description of the ovipositor and related structures of *Agabetes acuductus* Harris; (2), to provide further information about these structures among other genera of Laccophilinae; and (3), to examine the phylogenetic position of *Agabetes* and Laccophilinae. This represents an extension of my earlier research (Burmeister 1976) on this topic.

MATERIALS AND METHODS

Materials and methods used are described in Burmeister (1976). The terms and definitions used herein are explained in my previous paper. To facilitate comparison among illustrations, in this paper the structures and muscles are labelled in the same manner as in Burmeister (1976).

In addition to the taxa listed in Burmeister (1976), specimens of the following species were examined for this study.

Dytiscidae:Laccophilinae — *Neptosternus sumatrensis* Régimbart, *N. ornatus* Régimbart, *N. cosmani* Peschet, *N. jacobsoni* Zimmermann, *Laccodytes americanus* Peschet, *Laccophilus obliquatus* Régimbart, *L. maculosus maculosus* Germar, *L. maculosusus decipiens* LeConte, and *L. pictus* Castelnau; Colymbetinae — *Copelatus pulchellus* Klug, *C. erichsoni* Guer., *C. aethiopicus* Régimbart, *C. substriatus* Kirsch, *Lacconectes oceanicus* Régimbart, *L. laccophiloides* Zimmermann, *Matus bicarinatus* Say, and *Agaporomorphus knischi* Zimmermann; Amphizoidae — *Amphizoa lecontei* Matthews, and *A. insolens* LeConte.

OVIPOSITOR OF *AGABETES ACUDUCTUS* (HARRIS)

The general structure of the ovipositor of *A. acuductus* is shown in Fig. 6. In many aspects it is similar to other types of tactile ovipositor. The elongate gonocoxae are equipped with ventro-apical, small setae and in this character they are similar to those of females of Copelatini (Burmeister 1976). The elongate, narrow portions of tergum IX appear clasper-like and are connected with the gonocoxae by a ventral articulation. Tergum IX has a broad dorsal apodeme in the middle where the depressor (M32, Fig. 6) and levator muscles (M33, Fig. 6) have their origins. The origin of the depressor is on the inner side of tergum IX ventral to that of the levator. Both muscles are situated close together and are stretched out in a horizontal plane at rest. On the outer side of the process of tergum IX is the strong muscle (M15, Fig. 6) which acts as protractor of tergum IX.

The entire ovipositor is inserted into the gonocoxosternum (coxosternum). The gonocoxosterna (CS) are rectangular in shape (Figs. 6, 7a, 7c) with a ventroproximal appendix (A, Figs. 6, 7a-c). The ventromedial and distal borders of the gonocoxosterna are fringed with rows of short setae (Fig. 6a). At rest, the goncoxosterna are flat on top of sternum VIII. The small ventromedial appendix (A) of the gonocoxosternum is in contact with the unpaired, medial portion of genital appendages VIII (GH VIII, Figs. 6, 7). This is the same kind of articulation of gonocoxosternum with genital appendages VIII found in laccophilines (Fig. 4) (Burmeister 1976).

Genital appendages VIII are elongate and extend posteriorly nearly to the ventral papilla of the gonocoxae which have distal tactile setae (Fig. 7a). Genital appendages VIII are complex. They are fused into a single structure apically (Fig. 7b) but proximally there are three portions (Figs. 7a, b). The ventral portion is single and its distal end is differentiated by a small, membranous slit from the pair of lateral sclerites. The proximal tip of the ventral portion is articulated with the lateral appendages of the gonocoxosterna (Figs. 7, 8, 9). The more dorsal portion of this structure is paired proximally into lateral clasps. These clasps are elongated proximally past the point of articulation of the ventral portion (Figs. 7a, b). Distally, the fused portion of genital appendages VIII, is equipped with two, ventrolateral rows of small teeth extending to the tip. The dilator and depressor muscle (M28, Fig. 6) has its origin at the dorsoproximal margin of the gonocoxosternum.

The bursa copulatrix (bc, Fig. 7b) which receives the spermatophore during copulation, is elongated anteriorly with a well-developed system of musculature surrounding it. The receptaculum seminis is on the left side and is connected to the bursa by the ventral ductus receptaculi. The ductus seminalis originates at the receptaculum and extends posteriorly to the dorsal area of the divided vagina (va, Figs. 7b, d). At rest, the vagina ends distally between the three portions of genital appendages VIII.

PHYLOGENETIC CONSIDERATIONS

Plesiomorphic features of *Agabetes*.

The theory of cladistic analysis (Hennig 1950, 1981) specifies that primitive characteristics of any taxonomic unit can not be used to demonstrate its relationship with another group. Only derived or apomorphic features are used to document phylogenetic affinity. Nevertheless, the plesiomorphic characters of a group are important in the formulation of a ground-plan of structural features within a taxon.

The traditional placement of *Agabetes* within the subfamily Colymbetinae is based on the common presence of plesiomorphic character states. Among these are the following: (a) Size of specimens as indicated by total length which ranges from about 6.3 to 7.5 mm. (b) In specimens of *Agabetes*, the scutellum is visible externally (Fig. 1g). The scutellum is very small and anteriorly it is depressed to the level of the mesothoracic tergum and it is connected to the prothorax. (c) The metatarsomeres are not lobed posterolaterally. (d) Male specimens have pro- and mesotarsomeres I to III narrowly widened and supplied with numerous adhesive setae used to grasp the female during copulation. Character states (a) and (d) are widespread among members of Laccophilinae and Colymbetinae; character states (b) and (c) are widespread among members of Colymbetinae and Dytiscinae. Therefore these features are plesiomorphic based on out-group analysis.

Presumptive synapomorphies of *Agabetes* and Colymbetinae

Certain other character states of *Agabetes* could be interpreted as synapomorphies of *Agabetes* and Colymbetinae. One aspect of my study was to determine whether these are shared derived features or independently derived in both (or more) groups. These characters are eye shape and form of metepisternum.

Eye shape.— Two states: (1) inner margin rounded (Fig. 2a), (2) inner margin emarginate (Figs. 2b-f).

In many keys to subfamily and diagnoses of Colymbetinae (*e.g.*, Watts 1978) the emarginate eye of colymbetines is used as a diagnostic feature. The emargination is formed by a protrusion of the frons dorsally and distally from the antennal insertion (Figs. 3b-f). Common presence of emarginate eyes could be interpreted, incorrectly, as a synapomorphy of *Agabetes* + Colymbetinae.

Specimens of *Agabetes* have emarginate eyes but the feature is not prominent (Fig. 2b), whereas in most colymbetines (*e.g.*, Fig. 2c, Franciscolo 1979), this feature is more pronounced. More revealing, however, is the presence of an emarginate eye in specimens of Noteridae (*e.g.*, Fig. 2e), Laccophilinae (*e.g.*, Fig. 2f) and *Copelatus* Erichson (Fig. 2d). Among laccophilines, members of *Laccophilus* and *Neptosternus* Sharp have a prominent ocular emargination.

In summary, the presence of an emarginate eye is not a synapomorphy of *Agabetes* and Colymbetinae. The polarity of this character was not determined during this study. Study of further outgroup taxa would be needed for this.

Relative length of metepisternum.— Two states: (1) metepisternum extended to mesocoxal cavity and forming part of the lateral wall of mesocoxal wall (Figs. 3a, c-h); (2) metepisternum not attaining the mesocoxal cavity (Figs. 3b,i).

Sharp (1882:222-228, 967-972) used this character extensively in his classification of Dytiscidae. It is clear from Sharp's discussion of this character that he considered state 2 as plesiomorphic. Kavanaugh (1986: 84, 92, 94, 95) also discussed this character but assessed state 2 as apomorphic. Kavanaugh's polarity of this character is most likely correct.

Among Adephaga, Kavanaugh (1986) reported state 1 for one species of gyrinid (*Spanglerogyrus albiventris* Folkerts; Spanglerogyrinae), some dytiscids, fossils of Liadytidae, Triaplidae and *Necronectulus* Ponomarenko, amphizoids as well as eodromeine and protorabine carabids. In all other Adephaga examined by Kavanaugh, state 2 is present. Examination of the distribution of this character on his cladogram (Kavanaugh 1986, Fig. 22) suggests that his derived state is found in many, otherwise unrelated groups of Adephaga.

Among dytiscids, members of Vatellini (Hydroporinae) and Laccophilinae exhibit state 2 whereas all other dytiscids possess the first state. Therefore, *Agabetes* (Fig. 3a) and Laccophilinae (Figs. 3b, i) have opposite states and, if Kavanaugh is correct, laccophilines possess the apomorphic state and *Agabetes* is grouped with colymbetines based on a plesiomorphic state. Even if it could be demonstrated that Sharp's polarity is correct, the amount of homoplasy found in the distribution of character states would suggest that this is a weak, phylogenetic character.

Autapomorphic features of Laccophilinae

The 11 genera of Laccophilinae form a homogeneous group. The subfamily exhibits six synapomorphies, numbered below as they appear on Fig. 10.

1. Scutellum hidden in dorsal view. This feature may be convergent in members of Hydroporinae.
2. Metatarsus with single claw.
3. Metatarsomeres with posterolateral lobe.
4. Male specimens with parameres very short.
5. Female specimens with tactile portion of gonocoxae without setae and oriented dorsodistally (Fig. 4). The distal portion of the gonocoxosternum tactile.
6. Female specimens with ovipositor with large teeth on apicoventral margin (Fig. 4).

Relationship of *Agabetes* and Laccophilinae

Burmeister (1976) briefly discussed possible synapomorphies of *Agabetes* and Laccophilinae. These features are discussed in further detail below. They are numbered as they appear on Fig. 10.

7. Genital appendages VIII with fused, distal portion with two rows of ventral teeth and appearing saw-like (Figs. 4, 6, 7, 8). In specimens of *Agabetes* (Fig. 6) these teeth are not prominent. In other groups of dytiscids, serrate gonocoxae are known only from female specimens of *Ilybius* Erichson (Agabini, Colymbetinae) and *Hydrovatus* Motschulsky (Hydrovatini, Hydroporinae). However, in other features the female genitalia of *Ilybius* and *Hydrovatus* are markedly different from each other and from either *Agabetes* and Laccophilinae (see Burmeister 1976).

8. Genital appendages VIII composed of three elements proximally which are fused distally. Details of this structure differ among *Agabetes* (Fig. 7a) and Laccophilinae (Figs. 7c, 9b). However, in all other dytiscids studied to date, there is no separation of the genital appendages VIII proximally (Burmeister 1976).

9. Genital appendages VIII articulated with a ventroproximal appendix of gonocoxosternum. No other dytiscids have this type of articulation (Burmeister 1976).

Female specimens of *Agabetes* have this articulation at the distal margin of the ventral portion of genital appendages VIII (A, Fig. 6). In those of *Laccophilus*, in which the two lateral and the ventral appendages are fused for much of their length, the articulation is at the bases of the lateral arms (Figs. 4, 8). The condition found in *Laccophilus* may be more derived relative to that of females of other genera of laccophilines examined, for instance, those of *Neptosternus* and *Laccodytes* Régimbart [and possibly *Napodytes* Steiner also, see Steiner (1981)]. In representatives of these genera the fusion of the lateral and ventral arms is less than that expressed by *Laccophilus*. The articulation with the gonocoxosterna is near the proximal end of the ventromedial process (Fig. 8).

10. Tergum IX with a divided, median, dorsally elongate appendage Figs. 4, 6). This structure is the site of origin of the tergogonocoxal muscles and in no other groups of Dytiscidae are there divided areas of tergum IX which are similar.

11. Distal depressor muscle (M26) of genital appendages VIII (Figs. 4, 6). This muscle has its origin on the distal, ventromedial edge of the gonocoxa and inserts ventrally on the ventromedial process of genital appendages VIII. These muscles do not exist in other Dytiscidae (Burmeister 1976).

12. Origin of vaginal protractor muscle (M37) on lateral arms of genital appendages VIII (Fig. 6). Among other dytiscids, in particular *Copelatus*, this muscle acts to dilate the vagina and vaginal papilla. In *Agabetes* and Laccophilinae the vagina is between the unfused arms of genital appendages VIII. Therefore in these taxa (but not in *Laccophilus*) dilation of the vagina is brought about as muscles 37 pull outward on the lateral arms. This functional complex may be important for manoeuvering the saw-like ovipositor during endophytic, egg deposition.

Muscle 40 which is also a flexor of genital appendages VIII is known only from the genus *Laccophilus* and does not occur in other genera of laccophilines examined . Earlier, I suggested that M40 could be derived from M36 (Burmeister 1976: 209). In *Laccophilus*, muscle 36 inserts on genital appendages VIII near where all three arms are fused, whereas muscle 40 is more distal and it connects with the short, unfused portions of the lateral and ventromedial arms (Burmeister 1976, Fig. 27). Therefore muscle 40 may have been derived as a result of greater fusion of genital appendages VIII in *Laccophilus* relative to that of other laccophilines.

13. Origin of retractor muscle (M28) of genital appendages VIII. In most dytiscids, muscle 28 originates on the ventral edge of the gonocoxosternum posterior to the ventral apodeme and inserts on the posterior end of genital appendages VIII which are fused distally. In Laccophilinae and *Agabetes*, M28 extends from the dorsoventral edge of the gonocoxosternum and the posterior ends of the lateral arms of genital appendages VIII which are separated distally. In part, the different origin of M28 is due to the very elongate genital appendages. Nevertheless, this muscle has a dual function in *Agabetes* and Laccophilinae. It acts as a retractor muscle when the genital appendages are pulled posteriorly toward the resting position; toward the end of the retraction process, M28 acts to dilate the lateral arms and depress the genital appendages into the final resting position.

Autapomorphies of *Agabetes*

Many autapomorphies of *Agabetes* could be suggested [see Nilsson (1989) for discussion of some of these]. Other possible autapomorphies are (a) absence of lateral pronotal bead, (b) elongate protarsal claws of males, (c) presence of deep impressions laterally on sternum VIII (which is the apical, visible sternal sclerite). In addition, the median lobe of the male genitalia is elongate and has two dorsal appendages. However, this last character state may well be plesiomorphic.

RELATIONSHIPS AND CLASSIFICATION OF *AGABETES*

The function of the ovipositor of *Agabetes* is undoubtedly similar to that of Laccophilinae even though I have not observed oviposition of *Agabetes*. In both taxa, the genital appendages are differentiated into elongate sclerites with ventral serrations. These are adapted for cutting into aquatic plants during oviposition. In *Agabetes*, the gonocoxae appear to have retained a sensory function as indicated by presence of ventro-apical setae; the gonocoxae are used to assess the nature of the substrate prior to oviposition. In contrast, the gonocoxae of laccophilines lack sensory setae and are in the form of a knife-like cutting apparatus.

The reconstructed phylogeny of *Agabetes* and Laccophilinae is shown in Fig. 10. It is clear that these taxa are sister groups. The remaining problem is relative ranking of these two taxa. Nilsson (1989) chose to arrange these taxa into two tribes (Agabetini and Laccophilini) of a single subfamily (Laccophilinae).

An alternate arrangement would be to have both taxa at the rank of subfamily and I prefer this arrangement. In part, this is because of the number of apomorphic character states which isolate both taxa as a monophyletic unit and the number of synapomorphies expressed by each taxon individually. An important element of this is comparison of the number of apomorphies and synapomorphies shown by other tribes and subfamilies. For instance, comparison of Fig. 48 of my previous analysis (Burmeister 1976) and the present Fig. 10 suggests that each of these taxa (*Agabetes* and Laccophilinae) is as distinctive as are the other subfamilies of Dytiscidae (Hydroporinae, Colymbetinae and Dytiscinae). An important consideration is that all of these apomorphic states are based on a single functional complex of characters (female ovipositor, associated muscular and apical abdominal segment). However, this relationship remains a preliminary hypothesis and is in need of further study. Examination of other functional complexes of characters may necessitate modifications of the relative rank of these taxa.

ACKNOWLEDGEMENTS

I express my gratitude to my colleague, Dr. G. Scherer, for the loan of specimens of Dytiscidae and to my wife, Hedwig Burmeister, for her helpful comments and for proof-reading this manuscript together with Dipl. biol. F. Foeckler. Also, Dr. R. E. Roughley, of Winnipeg, assisted in editing the manuscript.

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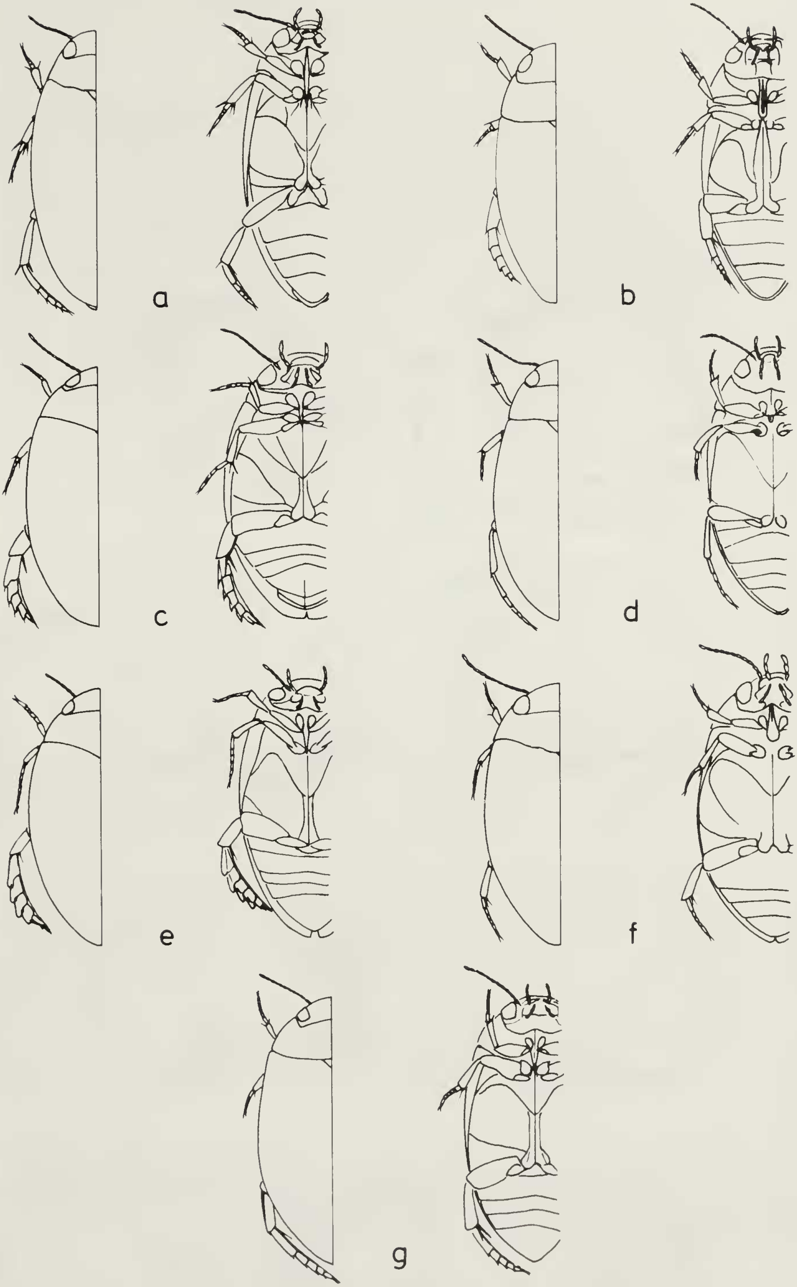

Fig. 1. Dorsal (left) and ventral (right) view of various females of Dytiscidae. (a), *Lancetes lanceolatus* Clark; (b), *Matus bicarinatus* Say; (c), *Laccophilus decipiens* LeC.; (d), *Agaporomorphus knischi* Zimmermann; (e), *Laccophilus maculosus* Germ.; (f), *Lacconectes laccophiloides* Zimm.; (g), *Agabetes acuductus* (Harris).

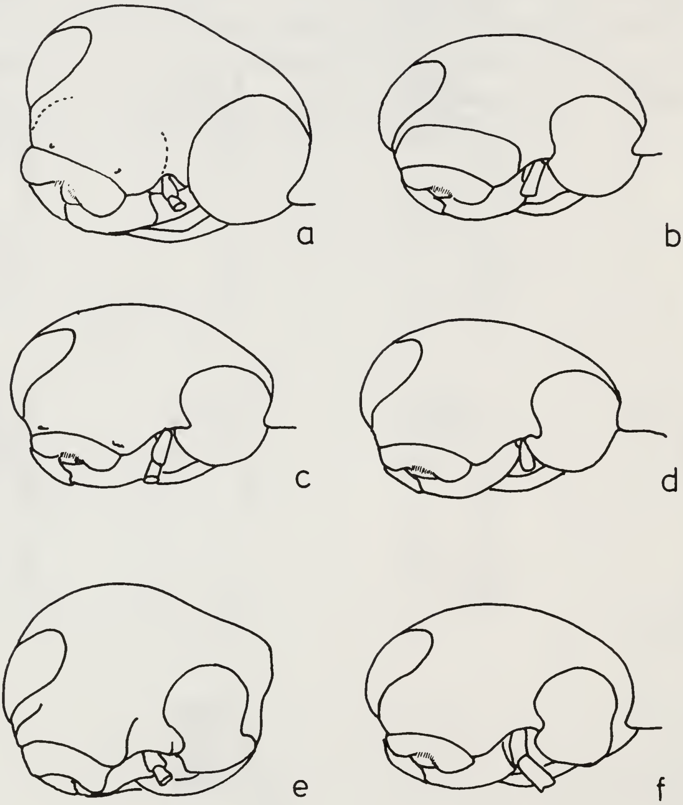

Fig. 2. Anterolateral view of head of various species of Hydradephaga. (a), *Cybister tripunctatus* Oliv. (redrawn from Franciscolo 1979); (b), *Agabetes acuductus* (Harris); (c), *Meladema coriaceum* Cast. (redrawn from Franciscolo 1979); (d), *Copelatus haemorrhoidalis* (F.); (e), *Noterus clavicornis* (Deg.); (f), *Laccophilus hyalinus* (Deg.).

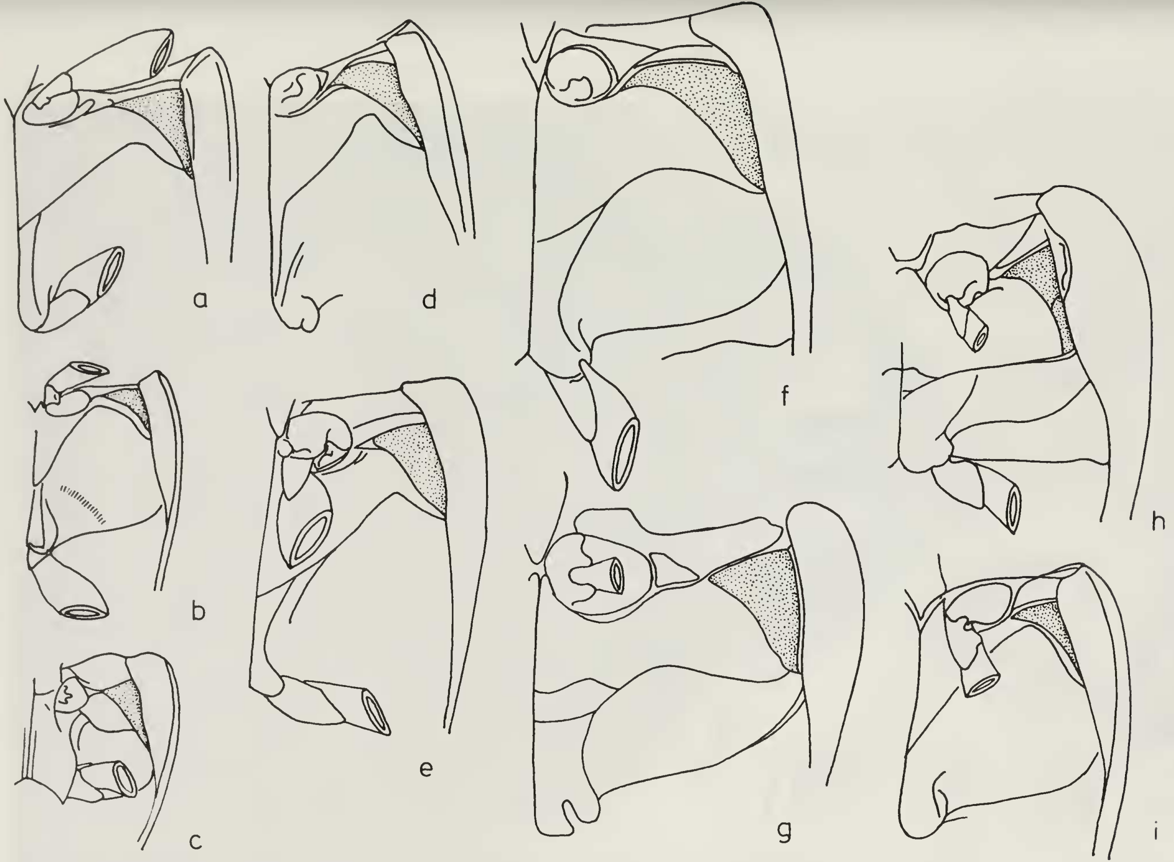

Fig. 3. Ventral view of meso- and metasternal area of various species of Hydradephaga. Metathoracic episternum stippled. (a), *Agabetes acuductus* (Harris); (b), *Laccophilus hyalinus* (Deg.); (c), *Noterus clavicornis* (Deg.); (d), *Copelatus haemorrhoidalis* (F.); (e), *Scarodytes halensis* (F.); (f), *Agabus bipustulatus* (L.); (g), *Hygrobia tarda* Herbst; (h), *Amphizoa lecontei* Matthews; (i), *Laccodytes americanus* Pesch.

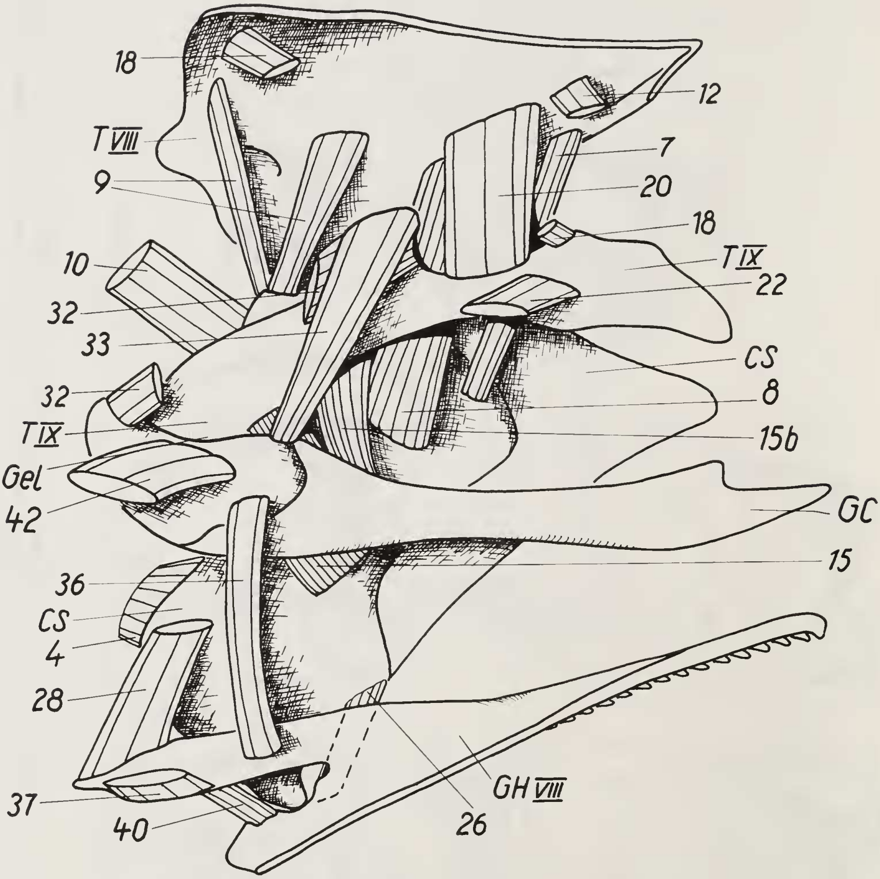

Fig. 4. Schematic view of female genitalia (last abdominal segment) of *Laccophilus hyalinus* (Deg.) with muscular system (modified from Burmeister 1976). Legend: CS- gonocoxosternum; GC- gonocoxa; Gel - articulation of tergum IX with gonocoxae; GH VIII- genital appendages of segment VIII; T VIII- tergum of segment VIII; T IX- tergum of segment IX which is divided into two lateral clasps together with gonangulum. Arabic numerals refer to muscles as follows: 4-10+32+33, gonocoxosternal muscles: 4 - retractor, 7-9 - levators, 10 - retractor, 32 - depressor, 33 - levator. 12 - retractor of membrane between terga VIII and IX. 15-26, muscles of tergum IX: 15-15b, depressors and protractors, 18 - retractor, 20 - levator, 22+26 - levators of membrane between lateral halves. 28+36+40, muscles of genital appendages VIII: 28 - depressor, 36 - extensor and levator, 40 - flexor. 37 - protractor and dilator of bursa copulatrix.

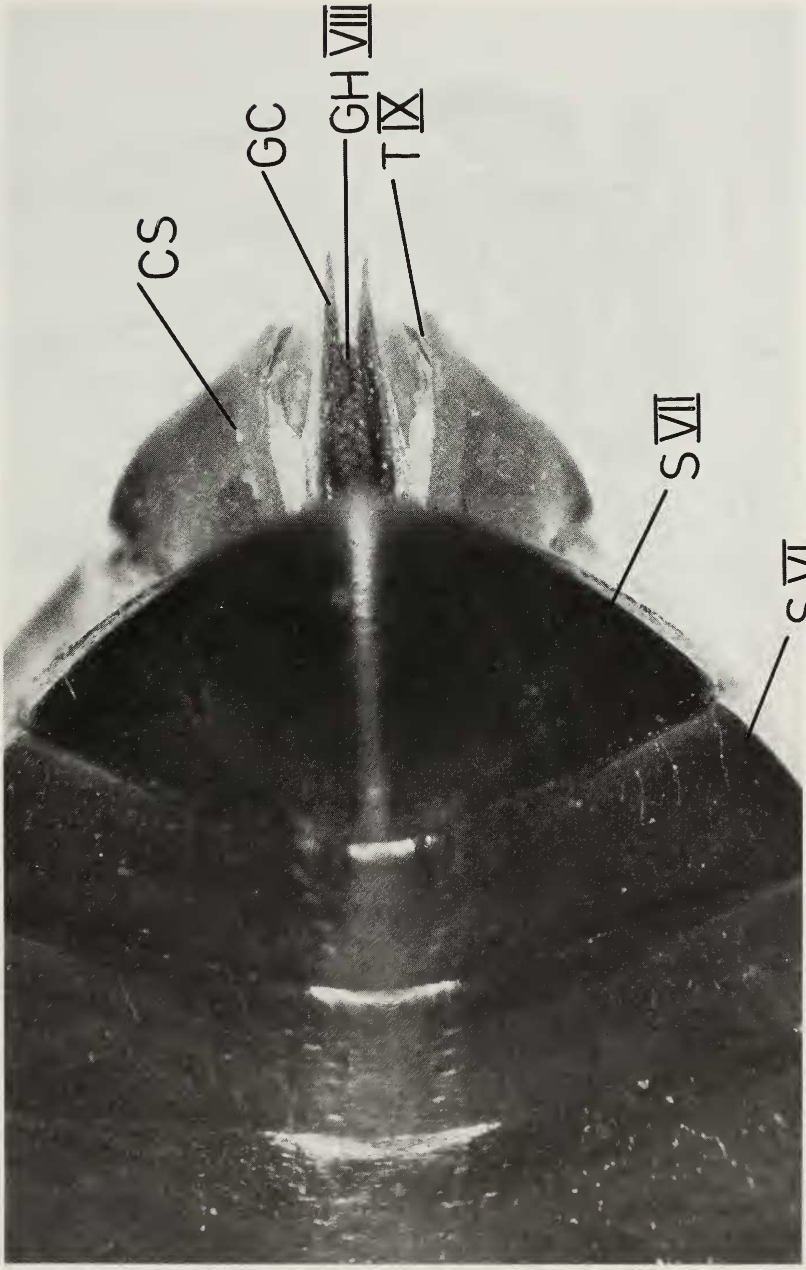

Fig. 5. Ventral view of the tip of abdomen of female *Agabetes acuductus* (Harris). The ovipositor is evaginated distally.

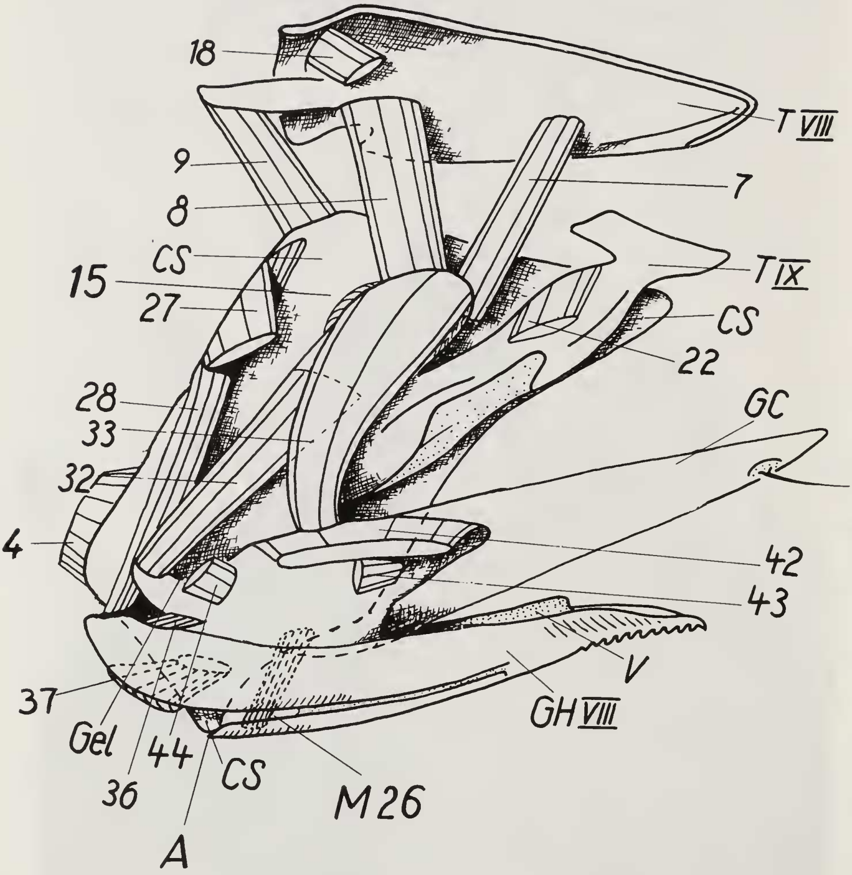

Fig. 6. Schematic view of female genitalia and last abdominal segment of *Agabetes acuductus* (Harris) with muscular system (modified from Burmeister 1976). Legend: A- articulation of gonocoxosternum with genital appendages VIII; CS- gonocoxo-sternum; GC- gonocoxa; Gel - articulation of tergum IX with gonocoxae; GH VIII- genital appendages of segment VIII; T VIII- tergum of segment VIII; T IX- tergum of segment IX which is divided into two lateral clasps together with gonangulum; V- papilla at vaginal opening. Arabic numerals refer to muscles as follows. 4-9, gonocoxosternal muscles: 4 - retractor, 7-9 - levators. 15-26, muscles of tergum IX: 15 - depressor and protractor, 18 - retractor, 20 - levator, 22+26 - levators of membrane between lateral halves. 27+32+33+42 - muscles of gonocoxa: 27+32 - depressors, 33 - levator, 42 - adductor. 28+36, muscles of genital appendages VIII: 28 - depressor, 36 - extensor and levator. 37 - protractor and dilator of bursa copulatrix. 43+44, vaginal muscles: 43 - protractor, 44 - dilator.

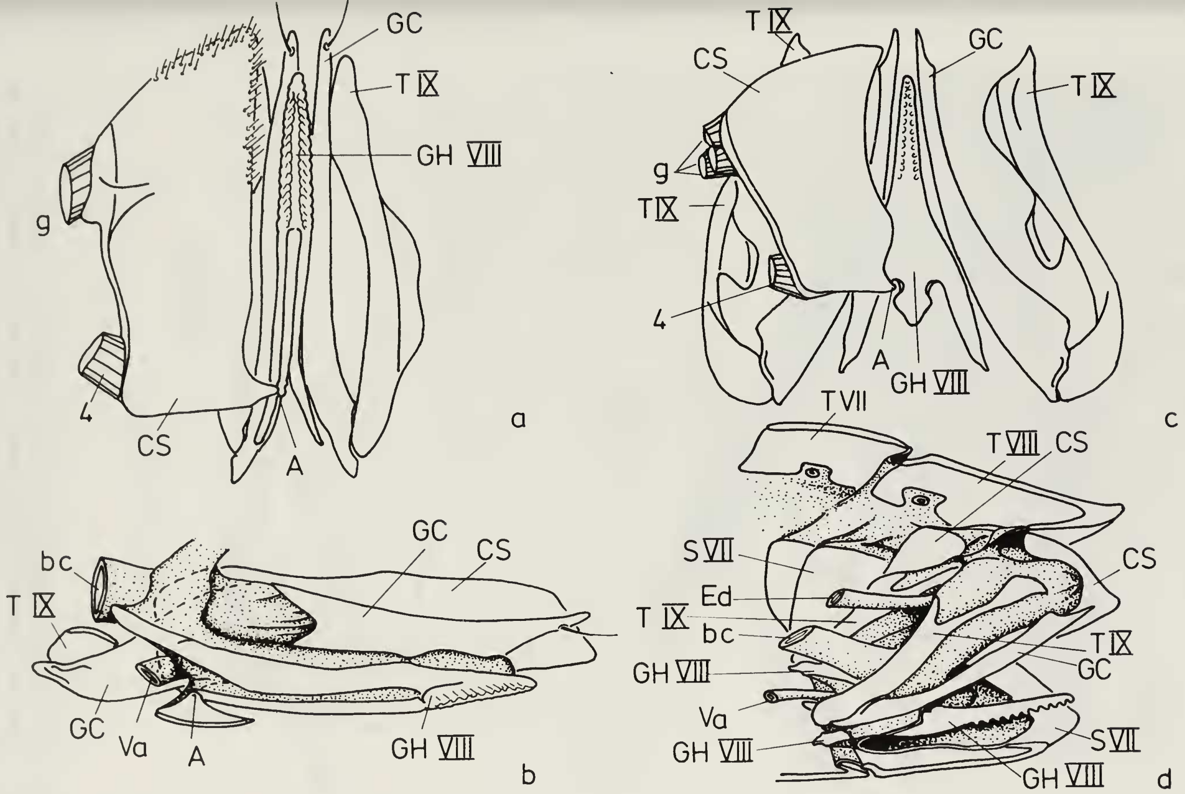

Fig. 7. Female genitalia of *Agabetes acuductus* (Harris) (a, b) and *Laccophilus* Leach (c, d). Ventral view (a, c) of sclerites and lateral view (b, d) of the sclerites and genital ducts in resting position. Legend: A - articulation of gonocoxosternum and genital appendages VIII; bc - bursa copulatrix; CS- gonocoxosternum; Ed - end of gut; g - levator of gonocoxosternum; GC- gonocoxa; GH VIII- genital appendages of segment VIII; S VII- sternum of segment VII; T VII-IX- terga of segments VII-IX; Va- vagina. 4 - retractor muscle of gonocoxosternum.

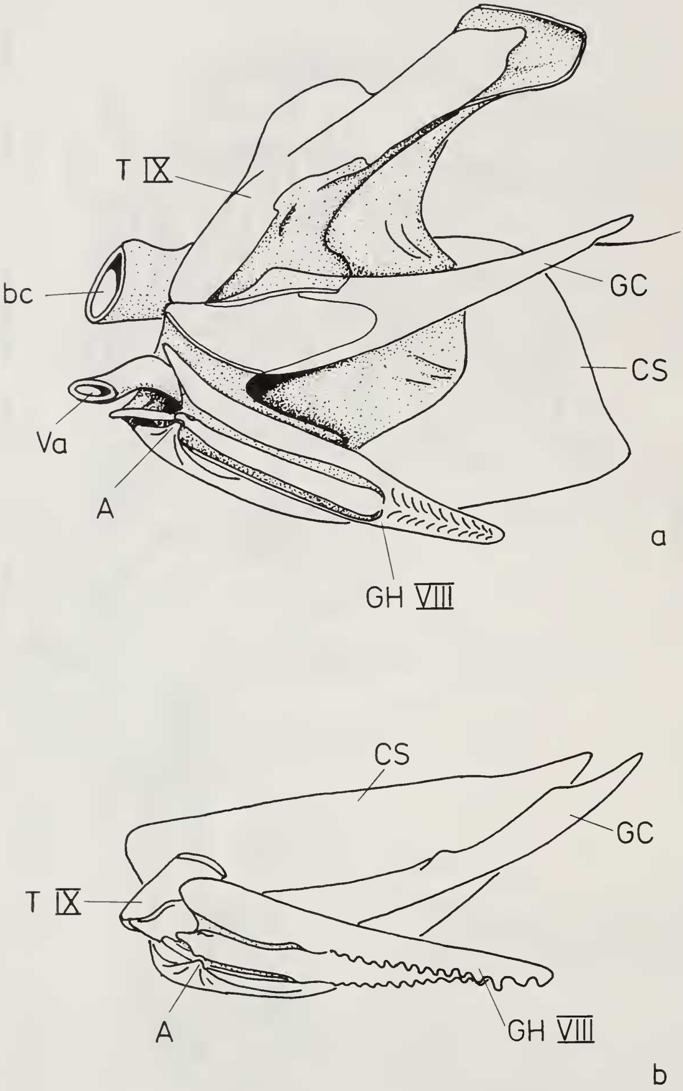

Fig. 8. Ventrolateral view of the appendages of female genitalia of (a) Agabetes acuductus (Harris) and (b) *Neptosternus sumatrensis* Rég. Legend: A- articulation of gonocoxosternum and genital appendages VIII; bc- bursa copulatrix; CS- gonocoxo-sternum; GC- gonocoxa. GH VIII- genital appendages of segment VIII; T IX- tergum of segment IX which is divided into two lateral clasps together with gonangulum; Va- vagina.

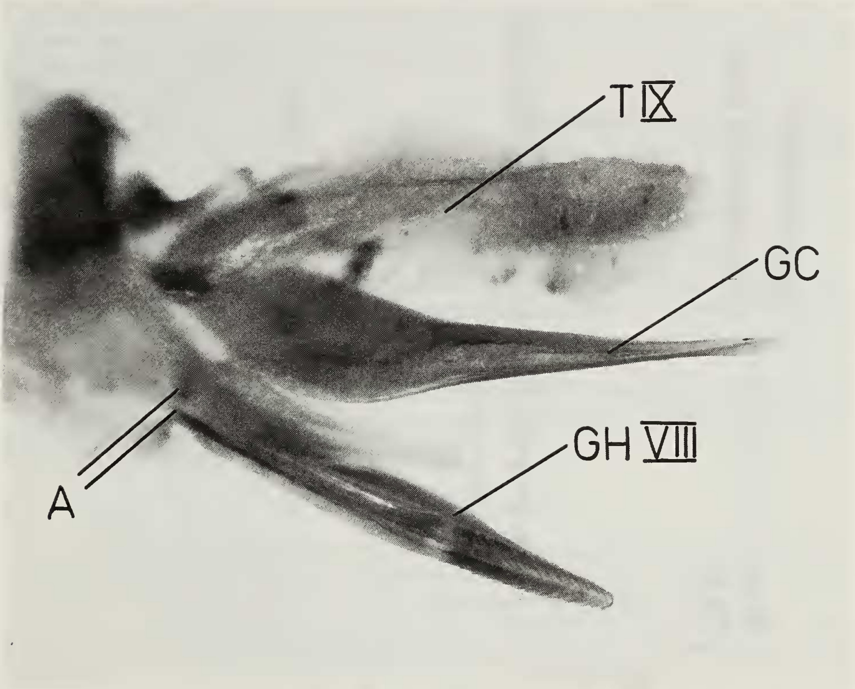

Fig. 9. Ventrolateral view of ovipositor of *Agabetes acuductus* (Harris). Legend: A- articulation of gonocoxosternum and genital appendages VIII; GC- gonocoxosternum.; GH VIII- genital appendages of segment VIII; T IX tergum of segment IX which is divided into two lateral clasps together with gonangulum.

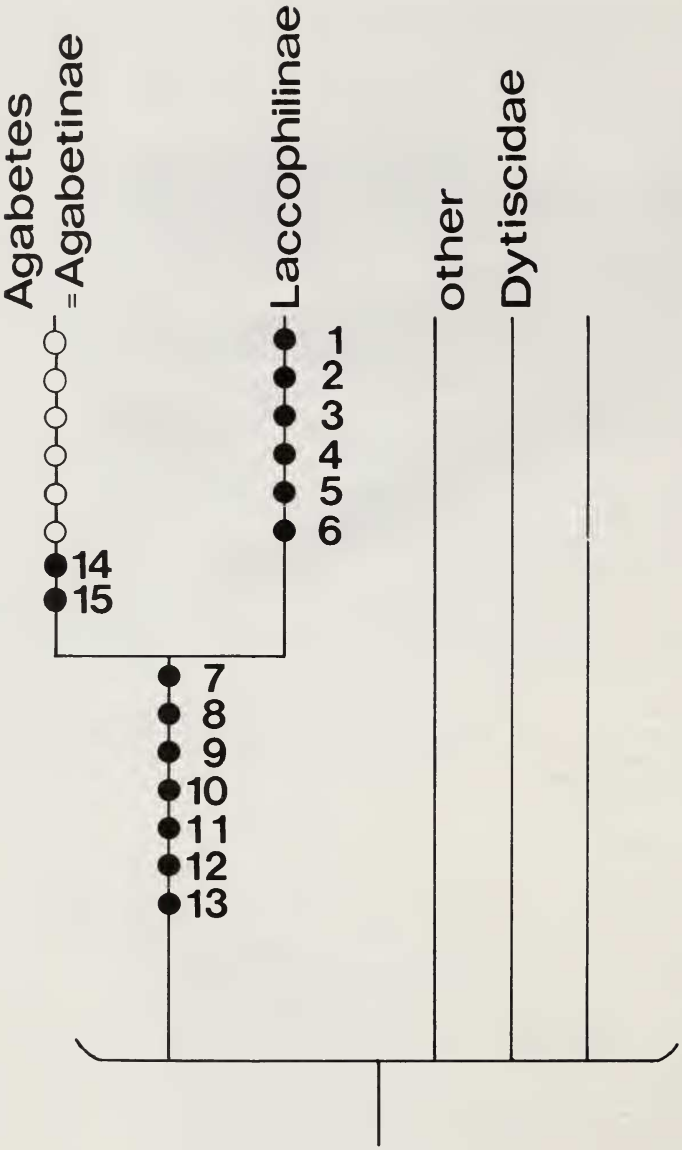

Fig. 10. Sister-group relationship of *Agabetes* Crotch and Laccophilinae shown by apomorphies (7 - 13), autapomorphies of Laccophilinae (1 - 6) and autapomorphies of *Agabetes* (14 - 15). Only characters of female genitalia are shown; for discussion of characters see text.